Predation by the beetle *Carabus granulatus* L. (Coleoptera, Carabidae) on soil macrofauna in grassland on drained peats

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Summary. Predation by *Carabus granulatus* on three invertebrate groups, Lumbricidae, larval Elateridae, and larval Tipulidae was examined using the serological method, and it was found that earthworms and larval tipulids were consumed. The frequency of detection of their antigens in the diet of predators was significantly correlated with the intensity of soil surface searching by these prey. Earthworms, probably the species active on the soil surface, such as *Dendrobaena octaedra* and *D. rubida*, represented a permanent food supply for *C. granulatus*. Larval tipulids were abundant only in some sites. They were intensely exploited by carabids in spring, when they were active on the soil surface. Larval elaterids did not occur on the soil surface, so they were rarely detected in the diet of carabids.

Key words: *Carabus granulatus*, gut contents, prey antigens, soil macrofauna, predation on Lumbricidae, soil surface

Indroduction

Carabus granulatus is the only representative of the genus *Carabus* in the meadows under study. In the spring-summer period, this predator occurs in all basic types of peatland habitats on drained fens in north-eastern Poland, where it is subdominant in carabid communities (Łukasiewicz, in prep.). As the largest invertebrate predator active on the soil surface, it can predate similarly large saprophages and herbivores of the epigean layer and, consequently, it can have an indirect effect on processes in which these invertebrates participate. However, trophic relations of *Carabus* species are poorly known under natural conditions.

Current knowledge of the food of *C. granulatus* and other representatives of this genus is based mostly on laboratory observations conducted in the 1920s and 1930s by German biologists. Based on the review by Hengeveld (1980a) of different *Carabus* species (*C. granulatus* was observed by Oertel (1924)), it may be concluded that their diet mostly consists of snails and earthworms. This author even includes the genus *Carabus* as specialized predators (Hengeveld 1980a).

Thiele (1977), reviewing work by other authors, mainly Jung (1940) and Scherney (1959), reports that *Carabus* species attack not only snails and earthworms but also most adult and larval insects. This is supported by more recent experiments conducted by Loreau (1986) on *Carabus problematicus*, and by my observations on *Carabus granulatus* (Łukasiewicz, in prep.). The latter predated all large earthworms species and larval insects supplied (Elateridae, Tipulidae). These data show that specialization of the beetles of the genus *Carabus* concerns selection of prey of a specific size rather than species. The adaption of *Carabus* species to feeding on large invertebrates is indicated by some morphological and

physiological traits, including the structure of mouth parts, alimentary canal, and especially external digestion (Sharova 1981; Evans & Forsythe 1985). The structure of the legs shows that these carabids prey on slowly moving invertebrates (Sharova 1981; Forsythe 1983; Evans & Forsythe 1984). Sharova (1981), who classified life forms of Carabidae based on morphological traits, included the genus *Carabus* in the group of slowly walking epigeobionts, preying on large, slowly moving epigean prey. Most species of this genus, including *C. granulatus* analysed in this paper, are generalists feeding on different groups of invertebrates.

The scarcity of data on the diet of the genus *Carabus* under natural conditions is a consequence of their external digestion which makes it impossible to perform a microscopic analysis of the content of their guts, commonly used for other carabids (e.g. Davies 1953; Sunderland 1975; Hengeveld 1980b; Pollet & Desender 1987). Direct observation of these beetles under natural conditions would also be very difficult because of their secretive life and mainly nocturnal foraging (Thiele 1977). Some data concerning the trophic niche of *Carabus* species can be obtained by a serological analysis of the guts, but this is not a frequently used method for beetles of this genus (Soboleva-Dokuchayeva 1975; Titova & Kuperstein 1976; Gruntal & Sergeeva 1989). This method also has its drawbacks. Among other things, it is not possible to determine the whole spectrum of food. Only the groups of prey against which specific antisera are produced can be identified. Nor can the absolute number of prey consumed be estimated (Benest 1986; Sunderland 1987; Hance & Renier 1987). It is possible, however, to identify certain groups of prey, most often to family. This is related to the degree of specificity of antisera, as both homologous antigens, originating from the tissues of the species used for serum production, and heterogeneous antigens, originating from related species, can give a positive reaction. Sensitivity of antisera to different species of the group that can be identified by using them, and also the detection time of these species in the food, can differ (Pickavance 1970; Boreham & Ohiagu 1978; Crook & Sunderland 1984). Moreover, it has been found that the detection period becomes longer as a result of recurrent feeding on the same prey species (Titova 1974).

Specificity of sera can be increased by using the absorption method, which reduces, however, the sensitivity of antisera (Dempster 1960; Sunderland & Sutton 1980), or by using special techniques of purification of antigens (Miller 1979). To examine predation on whole groups of prey, comprising all related species in a habitat, for example, from one family (taxocoenosis), less specific antisera, obtained in a simpler way, are used (Fox & MacLellan 1956; Soboleva-Dokuchayeva 1975; Sunderland et al. 1987).

It is therefore necessary to conduct a number of studies on the properties of antisera, species composition of potential prey in the habitat, and detection period of individual prey species under laboratory and field conditions to determine relative frequencies of feeding on different groups of prey. These additional tests can be more labour-consuming than basic studies. Despite these drawbacks, the application of serological methods to carabids with external digestion seems to be useful, taking into account scarcity of data on trophic relationship of these carabids under natural conditions.

In the study meadows, the invertebrates dominant by weight that could be an important source of food for carabids comprise earthworms (Lumbricidae), larval tipulids (Tipulidae) and larval elaterids (Elateridae) (Kajak et al. 1985; Andrzejewska et al. 1985; Wasilewska et al. 1985). These are large, relatively slow moving animals readily attacked and consumed by carabids, as indicated in laboratory experiments. As these are mainly soil invertebrates, they are likely to be available to beetles when emerging on the soil surface.

It is known that soil animals emerge onto the soil surface in search of food (Lee 1985; Mather & Christensen 1988). Among those analysed in this paper, this especially the case of earthworms. It is also known that when these invertebrates are present on the soil surface, they are exploited by different epigean predators. Many papers concern predation by vertebrate animals (MacDonald 1983; Lee 1985) but cases of earthworms exploitation by predatory epigean arthropods, including some species of carabid beetles, are also known (Loreau 1986, 1988; Pollet & Desender 1987).

The objective of the study described in this paper is to determine if the carabid *C. granulatus* preys upon the dominant groups of soil macrofauna under natural conditions, and whether this predation depends on searching of the soil surface by the prey population.

Materials and Methods

Study area

The study was conducted on the drained fen Wizna managed as meadows, located in the Narew valley, north-eastern Poland. Beetles were captured in three main types of meadows that differed in the peat derivation, and thus in habitat conditions and in numbers and structure of animal communities (Okruszko 1977; Pacowski 1977; Kajak et al. 1985). These were:
A — a wet meadow on the soil derived from little decomposed moss-peat, B — a moist meadow on the soil derived from moderately decomposed sedge-peat, C — a dry meadow on the soil derived from largely decomposed alder-peat.

Trapping of predators and prey

C. granulatus was trapped in 1983, 1985 and 1986. In the first year samples were taken from the three meadows (A, B and C) at the same time in the spring (3–13 May) and summer (22 July–1 August). Food of all individuals trapped was serologically analysed. Data from the summer sampling in meadow B are excluded from this analysis because of the low trappability and, consequently, small sample size for this period.
In the following years carabids were trapped in selected habitats (meadow C: 1–10 July 1985, and meadow A: 10–20 May 1986) to determine the detection period of prey antigens in the guts of carabids foraging under natural conditions, and also to collect carabids for laboratory experiments. Some randomly selected individuals were taken for serological analysis of the gut content immediately after trapping, as in 1983.
Pitfall traps 10 cm deep and 9.5 cm in diameter and without preservatives were used to catch carabids. The traps were put in the soil so that their edges were at the level of the soil surface. A total of 15 traps was run in each habitat for 120 hours over each trapping period.
In 1983 also epigean predatory macroarthropoda other than *C. granulatus* were captured and tested by using the same serological method. The results of these analyses are used to estimate and compare the effectiveness of different species of predators.
In 1983 and 1986 potential prey were captured in the same period as predators to determine the intensity of searching the soil surface by prey. Surface traps of a smaller diameter (6.5 cm) filled with a preserving liquid (ethylene glycol) were used for this purpose. From 10 to 15 such traps were run in each habitat. A unit intensity of area searching (trappability) was defined as the mean number of individuals captured per trap per 24 hrs. To estimate the density of prey in the soil, 15 samples from 25×25 cm squares 35 cm, deep were taken on each sampling date.

Preparation of antisera

To discover and identify prey antigens in the food of predators, three specific antisera were used: anti-Lumbricidae, anti-Tipulidae and anti-Elateridae, obtained from the blood of rabbits immunized against specific substances from tissues of the soil invertebrates mentioned above. To obtain the anti-Lumbricidae serum, rabbits were immunized with extracts from tissues of *Lumbricus rubellus* Hoffm. To obtain the anti-Elateridae serum, they were immunized with extracts from larval *Selatosomus* sp., and to obtain the anti-Tipulidae serum, they were immunized with extracts from larval *Tipula paludosa* Mg. The methods recommended by Boreham & Ohiagu (1978) were used.
Before using the antisera, their specificity was tested by using the extracts with which rabbits were immunized and also by using extracts from other species of potential prey.
Also the sensitivity of the antisera was determined, that is, the highest dilutions of the antigens at which positive reactions with sera were observed. The initial antigen concentration in extracts of prey tissue (dilution 1:1) was always 25 mg/ml fresh mass of homogenized prey.

Analysis of the food of predators

Extracts from entire guts of the beetles, together with their contents, were serologically analysed (Boreham & Ohiagu 1978). A technique of double immunodiffusion on agar gel was used (Ouchterlony 1948) with three antisera obtained from rabbits as described above to determine the frequency of prey detection in the diet of predators (proportion of individuals with antigens from prey tissues in the guts in the total number of individuals tested).

Detection period of prey in the diet of predators

The detection period of the antigens of prey consumed by *C. granulatus* under natural conditions was examined in two periods given above (1985, 1986). Extracts of the guts of these predators were serologically analysed using the method described at different times after trapping: 20 – 30 individuals immediately after trapping, 10 days after trapping and 20 days after trapping. Individuals not immediately analysed were fed on invertrebrates that did not show a positive cross reaction with antisera used in the experiment.
A separate group of individuals was used to determine the maximum time after which antigens derived from the prey consumed on one occasion under laboratory conditions could be detected in the guts of predators. These beetles were kept in the laboratory for the time needed to remove from their bodies the traces of their natural prey from the meadow. Like the other group, they were fed on invertrebrates the antigens of which did not produce cross reactions. Control tests after 60 days did not show any antigens detectable by the antisera. All these beetles were starved and then once allowed to feed to satiation on the prey species the detection period of which was examined. Some of these individuals (6 – 10) were tested every 12 hours for the presence of antigens of the prey species.

Results and Discussion

Sensitivity of antisera and detection periods of prey antigens

The results of the test confirmed the specificity of the antisera. The anti-earthworm serum gave positive reactions only with earthworm antigens *Lumbricus rubellus* Hoffm., *Dendrobaena octaedra* (Sav.), *D. rubida* (Sav.), and *Octolasium lacteum* (Oerley). The anti-elaterid serum positively reacted with antigens of elaterids in all developmental stages (*Selatosomus* sp., *Agriotes lineatus* L.), and the anti-Tipulidae serum positively reacted with antigens of tipulids in all developmental stages (*Tipula paludosa* Mg., *T. nigra* L., *Prionocera turcica* F.). No cross reactions were obtained with representatives of other families of Oligochatea (Enchytraeidae), Diptera (Chironomidae, Phrynaeidae, Ceratopogonidae, Empididae, Dolichopodidae, Tabanidae), Coleoptera (Carabidae, Hydrophilidae, Staphylinidae, Silphidae, Cantharidae, Dermestidae, Nitidulidae, Chrysomelidae, Curculionidae, Scarabaeidae); with other orders of insects (Collembola, Orthoptera, Dermaptera, Homoptera, Heteroptera, Hymenoptera, Lepidoptera) and other invertrebrate groups (Gastropoda, Isopoda, Opiliones, Araneae, Acarina, Diplopoda, Chilopoda) occurring in the study area.
Sensitivity of antisera was determined against all species of earthworms, larval elaterids and larval tipulids abundant in the study sites (Table 1). The tests showed clear differences in sensitivity of different antisera and also in sensitivity of the same antiserum against different prey species of the group that could be detected by these sera. The anti-earthworm and anti-elaterid sera were most sensitive against the homologous antigens (*L. rubellus*, *Selatosomus* sp.). In both cases, positive responses were observed at antigen dilutions of 1 : 32. Reactions of the anti-earthworm serum against antigens of the remaining earthworm species (*D. octaedra* and *D. rubida*) occurred at dilutions of 1 : 8, and those of the anti-elaterid serum against the antigens of the elaterid *A. lineatus* at dilutions of 1 : 16. The anti-Tipulidae serum was tested only against one homologous species. *T. paludosa*, which was abundant in the study sites. The sensitivity of this serum was lower, similar to the sensitivity of the

Table 1. Proportions of different prey species in particular prey families in the soil (as the total number of individuals from the soil samples) and active on the soil surface (as the total number of individuals from pitfall traps)

Species	Site					
	A		B		C	
	Soil	Surface	Soil	Surface	Soil	Surface
Lambricidae						
Lumbricus rubellus Hoffm.	71.0	7.4	0.0	0.0	0.0	0.0
Dendrobaena octaedra (Sav.)	5.4	71.3	71.0	87.0	98.5	100
D. rubida (Sav.)	19.8	17.0	20.0	4.3	0.0	0.0
others*	3.8	4.3	9.0	8.7	1.5	0.0
Elateridae L.						
Agriotes lineatus L.	39.1	—	66.7	—	100	—
Selatosomus sp.	60.9	—	33.3	—	0.0	—
Tipulidae L.						
Tipula paludosa Mg.	95.1	92.3	98.4	96.8	—	100
others**	4.9	7.7	1.6	3.2	—	0.0

Explanations: — not found in samples, * *Octolasium lacteum* (Derly), *Eiseniella tetraedra* (Sav.), ** *Tipula nigra* L., *Prionocera turcica* F.

anti-earthworm serum against heterogeneous antigens of earthworms of the genus *Dendrobaena* Eis. (1 : 8).

The detection periods of prey antigens in the guts of *C. granulatus* fed in the laboratory were examined only against homologous antigens. The detection periods were the longest for the prey species against which sera had the highest sensitivity (*L. rubellus*, *Selatosomus* sp.) (Table 2).

The detection periods of all of the most abundant prey species, the antigens of which could be detected in the food of predators by means of the antisera used, were examined for the carabid beetle *Pterostichus caerulescens* (L.). The maximum periods (in hours) after which prey antigens were present in 50 – 100% of individuals of this species, fed only once as described above, were as follows: earthworms: *L. rubellus* — 60, *D. octaedra* — 12 and *D. rubida* — 12; larvae of elaterids: *Selatosomus* sp. — 48 and *A. lineatus* — 24; larvae of tipulids: *T. paludosa* — 24. Although the detection period of prey in these beetles was generally shorter probably due to their smaller size and lower food consumption, as in the case of *C. granulatus* it was possible to find a dependence of the detection period on serum sensitivity (Łukasiewicz in prep.).

The detection period of prey in carabids under natural conditions could be determined only for earthworms (meadows A and C) and tipulids (meadow A), as only these two

Table 2. Detection of prey antigens in the diet of *C. granulatus* L. after a single feeding in the laboratory

Prey species	Time after feeding (hours)										
	0	12	24	36	48	60	72	84	96	108	120
Lumbricus rubellus Hoffm.	+++	+++	+++	+++	+++	+++	+++	+++	+++	+	—
Selatosomus sp. *l.*	+++	+++	+++	+++	+++	+++	+++	++	++	—	—
Tipula paludosa Mg. *l.*	+++	+++	+++	+++	+++	+	—	+	—	—	—

Explanations: +++ 100% positive response, ++ 50.0 – 99.9%, + 0.01 – 49.9%, — no positive response

Table 3. Detection frequency of prey antigens in the diet of *C. granulatus* L. in relation to the time after trapping in the field

Time of trapping	Site	Percent of individuals with antigens											
		Lumbricidae				Tipulidae				Elateridae			
		0	10	20	60	0	10	20	60	0	10	20	60
July 1985	C	46.7	53.3	46.1	0.0	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0
May 1986	A	60.0	46.7	43.3	0.0	36.7	26.7	6.7	0.0	0.0	0.0	0.0	0.0

Explanations: 0 — individuals tested immediately after capture, 10 — 10 days later, 20 — 20 days later, 60 — 60 days later

invertrebrate groups were the prey of a sufficiently large number of individuals (Table 3). The detection period of these prey remains in carabids on the meadows was relatively long, much longer than in individuals fed only once in the laboratory. For meadow C the proportion of individuals with earthworm antigens in the total number of carabids tested 20 days after trapping (46.1%) was similar to their proportion immediately after trapping (46.7%) and on meadow A is decreased only from 60% to 43%, respectively ($\chi^2 = 1.668$, df = 1, p > 0.1). It can thus be assumed that the detection period of earthworm traces in these predators was at least five times longer than that in individuals fed once in the laboratory. These differences were certainly much larger taking into account that the total detection period was not precisely determined under natural conditions. It has only been found that it was longer than 20 days and shorter than 60 days (Table 3).

Also carabids in the laboratory were fed on earthworms of the homologous species, *L. rubellus*, the antigens of which were detected for the longest period, whereas in the field heterologous species *D. octaedra* or *D. rubida* could be the prey of carabids.

The detection period of tipulids in carabids living on meadow A was 10—20 days. After 20 days the frequency of the detection of antigens of these invertebrates significantly decreased ($\chi^2 = 7.954$, df = 1, p < 0.01). It was at least five times longer than in the laboratory (Tables 2 and 3).

Laboratory experiments conducted by Titova (1974) show that the detection period of prey in predators is extended after repeated consumption of prey. After a single feeding of spiders on heteropterans, or feeding repeated for several days, the detection period of prey antigens in spider extracts did not exceed 9 days. When the same prey was supplied for more than 20 days, the detection period extended up to 1—2 or even more months. Similar results were obtained for carabids (Titova 1974). Mechanisms underlying this phenomenon are unknown. The extension of detection period of prey after their repeated consumption by predators may be due to the deposition of trace antigens. Titova (1974) suggests that predators produce "antibodies" against repeated ingestion of prey proteins.

The results of Titova (1974) are confirmed by the present results. The detection period of earthworms and tipulids was extended in carabids in meadows where they fed repeatedly on these prey.

*Frequency of prey detection in the food of **Carabus granulatus** in the field*

All three selected groups of soil invertebrates occurred in the guts of *C. granulatus* as shown by the analysis of gut extracts (Table 4). These were mostly earthworm antigens. The frequency of detection of these invertebrates slightly differed, depending on the habitat and period, but it was always high (41.2—73.7%), and typically statistically significantly higher than the frequency of detection of the two other groups of prey, that is, Tipulidae (in meadows B and C, p < 0.001 for all the study periods, in meadow A, p < 0.001 in July 1983 and p < 0.1 in May 1986, chi-square test) and Elateridae (p < 0.01—0.001 for

Table 4. Detection frequency of prey antigens in the diet of *C. granulatus* L.

Site	Period	Number of individual tests	Percent of individuals with antigens		
			Lumbricidae	*Tipulidae*	*Elateridae*
A	May 1983	34	41.2	44.1	0.0
	July 1983	19	73.7	15.8	0.0
	May 1986	30	60.0	36.7	0.0
B	May 1983	33	42.4	0.0	6.1
C	May 1983	37	43.2	2.7	0.0
	July 1983	19	52.6	0.0	0.0
	July 1985	21	47.6	0.0	4.8
	Total	193	49.7	15.5	1.5

all meadows and periods, chi-square test) (Table 4). Tipulid antigens were mainly detected in beetles from meadow A in spring periods with frequency similar to the frequency of detection of earthworm antigens (about 40%) and significantly higher than the frequency of detection of elaterid antigens ($p < 0.001$, chi-square test (Table 4). The frequency of detection of tipulid antigens on the other meadows was small and not significantly different from the frequency of detection of elaterid antigens (Fischer test, $p > 0.1$). The latter were the least frequently detected in the food of *C. granulatus*. Their antigens did not occur in specimens from meadow A, and they were only occasionally detected in specimens from the two other sites (Table 4).

The frequent detection of earthworm antigens in the diet of the carabids, considerably more frequent than that of tipulids and elaterids, can only be an effect of a frequent feeding of this predator on earthworms. It was assumed here that the sensitivity of the anti-earthworm serum was not higher, and the detection period of earthworm antigens was not longer than those of the larval tipulids and elaterids; that is, the probability of detection of earthworm antigens in the diet of predators was not higher than that of these two groups of soil larvae. This was especially the case for sites B and C where the genus *Dendrobaena* accounted for over 90% of the earthworm communities (Table 1).

The anti-earthworm serum showed a similar degree of sensitivity to the genus *Dendrobaena* as the other sera to the larvae of *T. paludosa* and to the larvae of *A. lineatus*. The detection period of earthworms of the genus *Dendrobaena* in the food of carabids *P. caerulescens* fed on this prey only once was even shorter than the detection period of larval Tipulidae and Elateridae (see above). Moreover, part of tipulid and elaterid antigens detected in carabid guts could derive from adult insects casually present on the soil surface and consumed by these predators. In the case of tipulids, this could occur only in summer, after the pupation of larvae and emergence of adults of these dipterans with annual developmental cycle, although at that period the frequency of detection of their antigens in the food of predators was already low. The results of this study show that mostly larvae in the period of intense searching of the soil surface were exploited (see below). This occurred in spring when pupae and adults were still absent from the meadows (Table 4).

On site A, in addition to the genus *Dendrobaena*, *L. rubellus* was also common (Table 1). The detection time of this species was much longer than that of most other prey species. However, the occurrence of *L. rubellus* on site A had no clear increasing effect on the total frequency of detection of earthworm antigens (Table 4). The proportion of individuals with earthworm antigens in the total number of *C. granulatus* captured on site A in the springs of 1983 and 1986 (41.2 and 60%) did not differ from their proportions on the other sites over all the trapping periods (42.4 − 52.6%).

A high frequency of detection of earthworm antigens in the food of carabids on all of the sites and in all of the periods (Table 4) provides evidence that earthworms are a permanent food source for these predators. A significant extension of the detection period of earth-

worm antigens, as shown by the test on sites A and C described in the preceding section, indicates that earthworms were frequently consumed also in the periods preceding their trapping.

Searching of soil surface by prey in relation to the diet of predators

Soil invertebrates emerging on the soil surface are available to epigean predators. A significant correlation was found between the intensity of soil surface searching by prey (earthworms, larval tipulids), as indicated by the rate at which they were caught in pitfall traps, and the frequency of detection of antigens of these two groups of invertebrates in the guts of carabids (Fig. 1). No such relationship was found between the densities of these two groups of prey in the soil and the frequency of the detection of their antigens in predators.

The intensity of soil-surface searching by earthworms varied greatly, and it was not correlated with earthworm densities in the soil. At the highest density of these invertebrates (131.7 ind. m^{-2} on site A in May of 1983) their trappability in pitfall traps was relatively low (0.019 ind. $trap^{-1}$ day^{-1}), whereas at a moderate density in July of 1983 it was extremely high (0.401 ind. $trap^{-1}$ day^{-1}) (Table 5). The density of earthworms on site C was so small, that in July of 1983 they were absent from soil samples. But in the same period, the intensity of soil surface searching by earthworms was 0.058 ind. $trap^{-1}$ day^{-1} (Table 5).

Earthworms search the soil surface under suitable microclimatic (humidity and thermal) conditions, mostly at night (Lee 1985; Mather & Christensen 1988). At that time they are exposed to epigean predators feeding at night (Loreau 1986, 1988; Pollet & Desender 1987). This group of predators includes *C. granulatus* (Thiele 1977).

Not all species of earthworms occurring on the study sites emerged from the soil, and thus were available to epigean carabids. Two species can be included in the group of surface earthworms, *D. octaedra* and *D. rubida*. This is in accordance with the classification of life-forms of earthworms proposed by Perel (1979).

The joint proportion of these two species in the total number of earthworms captured by the pitfall traps ranged from 89.3 to 100%, depending on the site. This high proportion was especially notable in the case of *D. octaedra*. Even on site A where the proportion of this species in the total number of earthworms recorded in the soil was relatively low (5.4%), it accounted for 71.3% of the earthworms captured in pitfall traps. On the other hand, *L. rubellus*, the dominant species on site A, accounting for 71% in the soil samples, classified
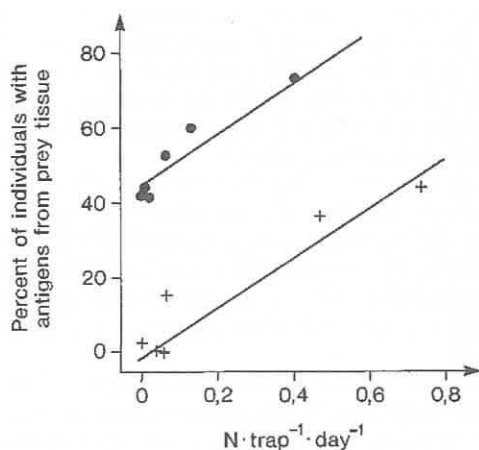

Fig. 1. Relationship between the intensity of soil surface searching by earthworms (●) or larval Tipulidae (+) and the frequency of detection of antigens of these invertebrates in the diet of *C. granulatus*. A significant correlation was found (Lumbricidae: $\tau = 0.733$, $p < 0.05$, Tipulidae: $\tau = 0.774$, $p < 0.05$, Kendal test)

Table 5. Mean densities ($N \cdot m^{-2}$) and intensity of soil surface searching ($N \, trap^{-1} \, day^{-1}$) by dominant groups of soil macrofauna

Site	Period	Macrofauna group					
		Lumbricidae		Tipulidae l.		Elateridae l.	
		density	searching activity	density	searching activity	density	searching activity
A	May 1983	131.7	0.019	33.1	0.731	77.7	0.00
	July 1983	78.0	0.401	6.4	0.061	129.0	0.00
	May 1986	80.2	0.130	40.0	0.470	91.0	0.00
B	May 1983	75.2	0.00	9.0	0.046	118.9	0.00
	July 1983	60.0	0.009	2.1	0.00	161.0	0.00
C	May 1983	20.0	0.008	0.0	0.00	199.5	0.00
	July 1983	0.0	0.058	0.0	0.004	125.1	0.00

in the soil-litter subgroup by Perel (1979), and occurring mainly in the mineral soil layer, was only occasionally recorded from the soil surface (Table 1).

These results suggest that mostly *D. octaedra* was exploited by carabids on the study sites. Examples of selective exploitation of earthworms by epigean predators can also be found in the literature. For instance, MacDonald (1983) reports several vertebrate species feeding on large earthworms such as *Lumbricus terrestris* L. Predatory epigean beetles can prey on smaller earthworms moving on the soil surface. For example, Loreau (1986, 1988) found that large nocturnal carabids preyed upon small epigean earthworms such as *Eisenia eiseni*, *D. rubida tenuis*, and *D. octaedra* on the site of a beech forest. These earthworms can be the staple food of some species of carabids in the periods of low availability of other prey, as they appear on the soil surface over the growing season (Loreau 1988).

Larval Tipulidae were represented in the study area mainly by one species *T. paludosa*. The proportion of this species in the total number of larvae collected from both soil samples and pitfall traps varied between 92.3 and 100%, depending on the site (Table 1). However, these invertebrates were abundant only on site A (Table 5). A high frequency of the detection of tipulid antigens in the guts of carabids in this habitat in spring (Table 4) was related to an intense searching of the soil surface by larval Tipulidae (Table 5). A marked decrease in the frequency of detection of their antigens in summer (Table 4) was releated to a decrease in numbers of the larvae (Table 5) during the period of pupation and emergence of adult forms.

Although the correlations between the intensity of soil surface searching by earthworms or larval Tipulidae and the frequency of detection of their antigens in the guts of carabids were statistically significant, the frequency of earthworm detection was higher than that of Tipulidae at a similar intensity of area searching by these two groups of prey (Fig. 1). This phenomenon can be explained by a more frequent feeding on earthworms in the period preceding the trapping of carabids, which accounted for the extension of the detection period of prey antigens in predators, as discussed in the preceding section. Earthworm antigens were detected in about 40% of *C. granulatus* (Table 4) even in the periods of a very low stability of these invertrebates, that is, when they did not occur on the soil surface (Table 5). These were probably traces of recurrent consumption of earthworms in earlier periods. With increasing intensity of area searching by prey, the proportion of carabids in which prey antigens were detected also increased (up to 73%). In these periods of increased earthworm availability, the guts of predators contained not only "trace" antigens but also antigens that appeared shortly after prey ingestion. Larval tipulids were probably less frequently eaten by carabids than earthworms, as indicated by the fact that tipulid antigens were frequently detected only when their area searching was very intense. In the periods of a

low availability of these prey, they were detected only in few carabids, which means that "trace" antigens rarely occurred.

The third group of the potential prey of *C. granulatus* discussed here, larval Elateridae, occurred in high densities on all the study meadows (Table 5). However, they did not emerge onto the soil surface — no individual was captured in the pitfall traps (Table 5). Thus, larvae, like pupae of these beetles, were not available to the epigean *C. granulatus*. It cannot be excluded that antigens detected in a small number of individuals derived from adult elaterids that could become the prey of these carabids when being on the soil surface.

Carabus granulatus in the group of species reducing earthworm numbers

Carabids exploiting soil invertebrates available on the soil surface can have an effect on numbers and dominance structure of the communities of these animals. The methods used in this study precluded a quantitative estimate of the effect of *C. granulatus* on the prey population. However, the results of the currently conducted experiment in the sedge meadow (site B) show that predatory epigean arthropods, including mainly beetles, considerably reduce numbers of earthworms moving on the soil surface. Elimination of these predators from tight enclosures, and limitation of their access to these enclosures for one year accounted for an increase in genus *Dendrobaena* by 53.3—57.0% as compared with not enclosed areas with a free access to predators. No such effect of predators was recorded on those earthworms rarely searching the soil surface, such as *L. rubellus* and *O. lacteum* (Łukasiewicz, in prep.).

An analysis of the food of all more abundant epigean predators in the study area (conducted in May and July, and also in October 1983, Łukasiewicz in prep.) has shown that the genus *Dendrobaena* could be reduced not only by *C. granulatus* (earthworm antigens were found in 49.7% of the individuals tested, n = 195) but also by the following carabids: *Pterostichus nigrita* (Fabr.) (44%, n = 125), *P. vulgaris* (L.) (43.8%, n = 128), *P. caerulescens* (L.) (12.4%, n = 419), *Harpalus rufipes* (De Geer) (10.8%, n = 37), *Amara similata* (Gyll.) (5.6%, n = 126), *A. communis* (Panz.) (3.5%, n = 57), *Clivina fossor* (L.) (4.5%, n = 22), and by less abundant predators (n = 1—9) such as *P. anthracinus* (Ill.), *Anisodactylus binotatus* (Fabr.), *Agonum sexpunctatum* (L.), *Elaphrus cupreus* (Duft., *Calathus melanocephalus* (L.), and *Synuchus nivalis* (Panz.); Staphylinidae: *Ocypus aenocephalus* Deg. (33.3%, n = 27), *Philonthus fuscipennis* (Mannh.) (9.9%, n = 91), *Ph. varius* (Gyll. (8.8%, n = 57); Cantharidae l. (22.1%, n = 298). Other groups of epigean predators had little effect on the reduction of earthworm abundance because they consumed these invertebrates on rare occasions (Araneae — Lycosidae, 1.3%, n = 238), or because they occurred in low numbers on the soil of the study meadows (Chilopoda, Opiliones, Heteroptera) (Łukasiewicz, in prep.).

As no data were available on absolute numbers of predators, a comparative analysis was made of the effects of different species on earthworm populations. For this purpose an effectiveness coefficient was used (Titova & Egorova 1978; Uzenbaev 1984) based on the proportion of individual species in the total number of predators trapped, and the frequency of consumption of earthworms by these species (percentage of individuals with earthworm antigens) (Table 6).

In the spring-summer period, *C. granulatus* was the most efficient predator species because it frequently consumed earthworms (41.2—73.7%), although its proportion in this group of predators was not high (1.1—11.9). In particular, this was the case in meadow A, where this species reached highest values of the effectiveness coefficient, similar to those of the dominant carabid *P. nigrita* and the dominant staphylinid *S. erythropterus*. In meadow C, only *P. caerulescens* was more effective in spring than *C. granulatus*, although it did not feed on earthworms very often (7.2—19.5%). Its effectiveness was due to its high dominance in the community of predators searching the meadow (24.0—43.7%). In meadow B, *C. granulatus* was relatively least important, whereas the beetles of the family Staphylinidae

Table 6. The effect of epigean predators on earthworm populations

Species	Site														
	A						B			C					
	May 1983			July 1983			May 1983			May 1983			July 1983		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Carabus granulatus L.	11.9	41.2	490	9.1	73.7	671	3.5	42.4	148	6.0	43.2	259	1.1	52.6	58
Pterostichus vulgaris (L.)	0.0	—	0	6.1	50.0	305	0.0	—	0	0.0	—	0	5.0	43.8	219
P. nigrita (Fabr.)	16.7	40.0	668	24.2	35.3	854	1.8	46.9	84	0.5	25.0	13	0.3	0.0	0
P. caerulescens (L.)	4.8	12.4	60	0.0	—	0	5.3	11.9	63	43.7	7.2	315	24.0	19.5	468
Harpalus rufipes (De Geer)	0.0	—	0	0.0	—	0	0.0	—	0	0.5	10.5	5	4.7	11.8	56
Amara similata (Gyll.)	4.8	5.6	27	0.0	—	0	0.0	—	0	13.1	4.0	52	18.5	7.5	139
A. communis (Panz.)	0.0	—	0	0.0	—	0	5.8	4.0	23	0.0	—	0	0.0	—	0
Staphylinus erythropterus L.	30.9	15.4	475	30.3	30.0	909	0.5	50.0	25	0.5	0.0	0	0.0	—	0
Philonthus fuscipennis (Mannh.)	9.9	25.0	238	9.1	0.0	0	79.7	10.0	797	31.7	5.0	158	41.4	5.0	207
P. varius Gyll.	9.5	0.0	0	12.1	0.0	0	3.6	7.7	23	2.1	20.0	42	1.4	0.0	0
Others	11.9	20.0	238	9.1	0.0	0	0.5	0.0	0	1.8	0.0	0	3.6	23.1	83

Explanations: 1 — percentage of a single species in the group of predators feeding on earthworms antigens, 2 — percentage of individuals with earthworm antigens, 3 — comparative coefficient of the effectiveness of predation on prey populations

Ph. fuscipennis had a high value of the effectiveness coefficient and was present in this meadow in very large numbers (79.7%) (Table 6).

The study carried out in the same habitats in autumn show that the contribution of the carabid and staphylinid beetles to the exploitation of earthworms was low (Łukasiewicz, in prep.).

C. granulatus, which are spring breeders (Thiele 1977), almost did not search meadows at that time. Single individuals of this species were captured occasionally. The most important predators of earthworms in autumn were epigean larvae of beetles of the family Canthari-dae, which predominated the community of epigean predators feeding on earthworms (81.1 – 94.0%) in all the meadows under study (Łukasiewicz, in prep.).

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